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TEMPERATURE-MEDIATED CHANGES IN SEED DORMANCY AND LIGHT REQUIREMENT FOR *PENSTEMON PALMERI* (SCROPHULARIACEAE)

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Abstract—*Penstemon palmeri* is a short-lived perennial herb colonizing disturbed sites in semiarid habitats in the western USA. In this study seed was harvested from six native and four seeded populations during two consecutive years. In laboratory germination trials at constant 15 C, considerable between-lot variation in primary dormancy and light requirement was observed. Four weeks of moist chilling (1 C) induced secondary dormancy at 15 C. Cold-induced secondary dormancy was reversed by one week of dark incubation at 30 C. This warm incubation treatment also reduced the light requirement of unchilled, after-ripened seed. Fluctuations in dormancy and light requirement of buried seeds have been linked to seasonal changes in soil temperature. *Penstemon palmeri* germination responses to temperature appear to be similar to those of facultative winter annuals.

Key words: seed germination, Palmer penstemon, seed bank, induced dormancy, beardtongue, Penstemon palmeri.

Seed dormancy mechanisms function to ensure that germination is postponed until conditions are favorable for seedling survival (Fenner 1985). The level of dormancy of an imbibed seed is dependent upon its dormancy level prior to imbibition and on the environmental conditions to which it has been exposed in the imbibed state (Bewley and Black 1982).

Chilling, essential for breaking dormancy in seeds of many temperate species, induces varying degrees of secondary dormancy in others (Baskin and Baskin 1985). Conversely, warm temperatures increase and diminish dormancy in other species. These temperature-mediated changes in seed dormancy are related to the season in which seeds undergo germination and emergence. Thus, spring and fall germinators tend to have opposite responses to chilling and warm-temperatures regimes.

Penstemon palmeri Gray is a short-lived perennial herb native to the southern half of the Great Basin and adjoining regions of the western United States (Cronquist et al. 1984). It occurs across a fairly broad range in elevation (800–2750 m), colonizing relatively open, early successional sites such as roadcuts and washes. Individual plants produce large quantities of seed that remain viable for several years in storage (Stevens et al. 1981). Numerous populations have been successfully established through artificial seeding on a variety of sites outside its native range (Stevens and Monsen 1988). This versatility raises questions about the establishment strategy of this species. In this study the effects of moist chilling and warm incubation on seed germinability were determined under controlled laboratory conditions. The results are sufficiently clear to permit speculation about seedbed ecology and have led to the fieldwork necessary to confirm the conclusions drawn herein.

In laboratory trials on *P. palmeri*, Young and Evans (unpublished data, Great Basin Experimental Range, Ephraim, Utah) demonstrated that germination at a constant 15 C was not significantly lower than at any other constant or alternating temperature regime. Germination over a 28-day period was suppressed at mean temperatures below 10 and above 25 C. Allen and Meyer (1990) reported similar results in a study of three *Penstemon* species and suggested the possibility of cold-induced secondary dormancy in *P. palmeri*. Field sowing of this species is usually carried out in late fall and is based on the assumption that a cold treatment is required to break dormancy (Stevens and Monsen 1988).

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METHODS

Seed Acquisition

Ripened seeds were harvested from nine populations in 1986. Collections were made from eight of the original and one new population in 1987 (Table 1). Four of the populations were from roadside seedings outside the native range of this species. The genetic origin of the artificially seeded populations is unknown. Each collection was cleaned using standard techniques and stored in envelopes at 20 C (room temperature).

Viability Determination

An estimate of viability for each 1986 collection was obtained using a tetrazolium chloride (TZ) test. Four replications of 25 seeds from each collection were imbibed overnight. Each seed was pierced and placed in a 1% TZ solution at room temperature for 24 hours. Embryos were then evaluated for viability using established procedures (Grabe 1970).

Gibberellic acid (GA_3) effectively breaks dormancy in *P. palmeri* seeds (Young and Evans, unpublished data, Great Basin Experimental Range, Ephraim, Utah). Four replications of 25 seeds for each 1986 collection were imbibed in 250 mg L^{-1} GA_3. Germination temperature was a constant 15 C. Germination percentages, determined after 21 days, showed no significant differences between TZ estimates of viability and germination percentages in GA_3. Hence, germination in GA_3 was the only measure of viability employed with 1987 seed.

Experiment I

Experiment I was started on 1 June 1987. Mean time after harvest date was approximately nine months (Table 1). The experiment was designed to determine the effect of three temperature pretreatments on germination of seed from the nine 1986 collections under two light regimes. Pretreatments included: (1) chilling for 28 days at 1 C, (2) incubation for 7 days at 30 C, (3) chilling for 28 days at 1 C followed by incubation for 7 days at 30 C, and (4) no pretreatment. Germination temperature and duration following pretreatment was a constant 15 C for 21 days. The light regimes were a 12-hr photoperiod and constant darkness.

Each pretreatment-light regime combination was replicated four times for each of the nine collections. Replicates consisted of 25 seeds placed on top of two germination blotters in a 100 × 15-mm petri dish. Blotters were moistened to saturation with deionized water.

Experimental units assigned the same pretreatment and light regime were randomized in stacks of 10. A blank dish (blotters but no seeds) was placed on top of each stack that would receive light, ensuring that all seeds would receive light through the sides of the dish only. Light intensity inside the dishes was 25 microeinsteins m^{-2} sec^{-1} PAR. Each stack was enclosed in a plastic bag and loosely sealed with a rubber band to retain moisture and facilitate handling.

During pretreatment, stacks were placed in cardboard boxes, each of which was enclosed in an additional plastic bag. After pretreatment, stacks assigned the light regime were removed from their boxes and randomly arranged in the growth chamber directly beneath fluorescent lights. The remaining boxes were placed in the growth chamber and were not opened until the end of their germination period.

Seeds with radicle extension >1 mm were counted as germinated. Experience with this and other penstemon species has shown this to be a clear indicator of the initiation of seedling development. A germination percentage was determined for each replicate (dish). Germination percentages were arcsine transformed for statistical analysis. Experimental results were subjected to analysis of variance procedures appropriate to the completely randomized design. Because of the collection × treatment interaction in the analysis of variance, each collection and treatment was analyzed independently. Significant differences among treatment and collection means were determined using the Student-Newman-Keul (SNK) method.

Experiment II

A second experiment was started on 14 October 1987 using nine fresh (1987) collections (Table 1). Mean time from harvest was approximately one month. The objective was to determine the effect of 30 C (imbibed) on primary dormancy and light requirement of fresh seed. The methods were the same as those used in the first experiment with three exceptions: only one pretreatment was used (30 C), the length of the pretreatment was 14 days, and the length of germination was 28 days. Light and dark controls (no warm incubation) were again included.

TABLE 1. Location and harvest dates for 10 populations (18 collections during two years) of *P. palmeri*. All populations are in Utah except the Mountain Home population in Idaho.

Collection	Lat (N)	Long (W)	Elevation (m)	Harvest date 1986	Harvest date 1987
Snow's Canyon	37°12′	113°39′	1080		8/14
Browse	37°21′	113°15′	1350	8/22	8/14
Leeds	37°14′	113°21′	1050	8/8	8/14
Zion	37°14′	112°54′	1740	8/22	9/14
Kolob Road	37°16′	113°06′	1440	8/8	9/13
Utah Hill	37°08′	113°47′	1380	8/8	
Mountain Home[a]	42°57′	115°05′	930	8/13	8/27
Mercur Canyon[a]	40°25′	112°10′	1650	12/15	9/22
Salt Creek Canyon[a]	39°42′	111°45′	1740	9/10	10/10
Nebo Loop[a]	39°52′	111°40′	2100	10/26	10/10

[a]Artificially seeded populations from outside the natural range

RESULTS

Experiment I

Four weeks of chilling reduced germination in light significantly below the level of controls for six of the nine collections (Table 2). Incubation at 30 C caused no significant change for germination in light when compared to the control. When the four-week chill was followed by one week at 30 C, mean germination percentage was only slightly lower than that of the control. This indicates that incubation at 30 C effectively reversed the secondary dormancy induced by chilling. In addition, incubation at 30 C substantially increased the dark germination percentage over the dark control (Table 3). The 30 C warm incubation was much less effective in removing the light requirement when preceded by chilling.

Germination rate at 15 C was only slightly accelerated by chilling and warm incubation pretreatments (data not shown). Mean germination for the light control treatment after seven days was 15%, indicating that most essentially nondormant seeds required a considerable period of imbibition before germination was possible. Four weeks of chilling and one week of warm incubation increased the proportion of seeds that germinated by day 7 to 24 and 28%, respectively. However, a major fraction of the seeds still required more than one week of constant imbibition at 15 C to germinate.

Experiment II

In the first experiment there was a slight trend in the more dormant lots for germination to be higher after warm incubation relative to the control. The second experiment was conducted to determine if warm incubation could break the primary dormancy of fresh seeds.

Contrary to what was expected for fresh seed, only two of the nine 1987 collections showed significant primary dormancy (Table 4). The increase in germination percentage following warm incubation was significant when compared to the nonincubated light control for one of these collections. In the remaining collections, neither the light control nor the light, warm-incubated germination percentages were significantly different from total viability estimates determined by germination in GA_3.

The variation in dark germination was similar to that observed in the first experiment with after-ripened seed (Table 4). The effect of warm incubation on dark germination was not as clear as in the initial experiment. Germination of the warm-incubated seeds resulted in a mean net increase over nonincubated, dark controls of only 11%. Four of the nine collections showed significant increases, while one showed a decrease.

DISCUSSION

Moist chilling for four weeks caused varying degrees of secondary dormancy in *P. palmeri* seed collections. Incubation at 30 C clearly

TABLE 2. Germination response of nine after-ripened collections of *P. palmeri* seed to moist chilling (1 C for 28 days) and warm incubation (30 C for 7 days). The germination period was for 21 days at a constant 15 C with a 12-hr photoperiod. Germination in 250 mg L^{-1} GA_3 was used as an estimate of total viability for each collection.

	Mean germination percentage[a]				
		Pretreatment			
Collection	Control	1 C	30 C	1 C/30 C	GA_3
Browse	90a	41b	92a	86a	91a
Leeds	89a	38c	92a	73b	93a
Zion	72a	73a	80a	71a	81a
Kolob Road	95a	63b	90a	86a	97a
Utah Hill	89a	39b	88a	78a	82a
Mountain Home	88ab	65b	89ab	87ab	92a
Mercur Canyon	86b	21c	87b	81b	99a
Salt Creek Canyon	58b	55b	80ab	72b	92a
Nebo Loop	75a	38b	84a	80a	89a
Means	82b	48d	87b	79c	91a

[a]Within a collection, means followed by the same letter are not significantly different at the $p < .05$ level (SNK).

broke cold-induced secondary dormancy in after-ripened seed, and there is some indication that it can reduce levels of primary dormancy as well. The warm-induced reduction in light requirement was less pronounced for fresh compared to after-ripened collections.

The response of *P. palmeri* seeds to moist chilling and warm incubation parallels those observed for fall germinators (winter annuals) (Baskin and Baskin 1985). This is supported by the lack of primary dormancy in freshly harvested seeds. Nevertheless, a significant portion of the seeds was not induced into secondary dormancy during chilling. This suggests that late winter/early spring germination of some seeds is likely. It is of little surprise that recently emerged seedlings were found in *P. palmeri* populations in both spring and fall. Such bimodal germination patterns are typical of facultative winter annuals (Baskin and Baskin 1985) and would be selected for in unpredictable habitats where the best season for seedling survival may differ from year to year (Silvertown 1984). Such germination patterns would also be adaptive for species that colonize different kinds of habitats with varying degrees of threat from frost and drought. Both situations occur within the range of *P. palmeri*.

Given its small seed size (Plummer et al. 1968), a light requirement for germination of *P. palmeri* is not surprising (Fenner 1985). The level of active phytochrome in dry seeds and, subsequently, light sensitivity is strongly influenced by conditions during ripening (Cresswell and Grime 1981, Gutterman 1982) and may vary considerably among the seeds of a single plant (Silvertown 1984). The *P. palmeri* seeds in these experiments demonstrated three levels of response to light, suggesting variable levels of total or active phytochrome in the seeds. Some seeds germinated in the dark while others required light, and a few remained dormant even with light. The proportion of seeds that could germinate in the dark was increased by incubation at 30 C (Table 3).

Light sensitivity can be altered by temperature shifts during seed imbibition (Toole 1973, Franklin and Taylorson 1983). This may be due to temperature effects on the production, destruction, or dark reversion of phytochrome. Temperature shifts may also alter other factors associated with phytochrome action, thus resulting in an increase or decrease in light sensitivity. Hendricks and Taylorson (1978) suggested that temperature effects on phytochrome action in seeds may be due to changes in membrane fluidity. It is likely that the effects of temperature on light sensitivity in seeds are a result of more than one process acting in concert.

A light requirement may help determine season of germination for buried *P. palmeri* seeds. Habitats with adequate winter snows provide enough moisture for spring germination of surface seed. Long periods (8–16 weeks) of

TABLE 3. The effect of chilling (1 C for 28 days), warm incubation (30 C for 7 days), and chilling followed by warm incubation on the light requirement of nine after-ripened collections of P. palmeri. The germination temperature was 15 C.

	Germination percentage[a]				
	Light	Dark			
Collection	Control	Control	1 C	30 C	1 C/30 C
Browse	90a	56c	32d	75b	17e
Leeds	89a	45c	16d	68b	13d
Zions	72a	37c	35c	55b	24c
Kolob Road	95a	49c	31e	77b	34c
Utah Hill	89a	41b	23b	70a	33b
Mountain Home	88a	54b	59b	87a	65ab
Mercur Canyon	86a	42b	6c	83a	38b
Salt Creek Canyon	58a	26b	34b	76a	46ab
Nebo Loop	75a	12c	8c	61a	35b
Means	82a	40c	27e	72b	34d

[a] Within a collection, means followed by the same letter are not significantly different at the $p = .05$ level (SNK).

TABLE 4. Primary dormancy, light requirement, and the effect of warm incubation (14 days at 30 C) on the germination of nine fresh collections of P. palmeri seed. The germination period was 28 days at 15 C. Light treatments received a 12-hr photoperiod. Germination in GA_3 (250 mg L^{-1}) was used as a measure of viability for each collection.

	Germination percentage[a]				
	Control		30 C pretreatment		
Collection	Light	Dark	Light	Dark	GA_3
Snow's Canyon	94a	31b	85a	34b	97a
Browse	86a	25c	80a	53b	93a
Leeds	92a	35b	91a	51b	92a
Zions	70a	38b	72a	24c	74a
Kolob Road	83a	30b	88a	17b	87a
Mountain Home	96a	56b	87a	66b	94a
Mercur Canyon	87a	58b	87a	76a	94a
Salt Creek Canyon	77bc	45d	86b	67c	98a
Nebo Loop	55b	16c	74a	40b	81a
Means	82b	37d	83b	48c	90a

[a] Within a collection, means followed by the same letter are not significantly different at the $p = .05$ level (SNK).

moist chilling reduce the time needed for germination to occur, thus increasing the chances of spring-germination and seedling establishment from seeds not induced into secondary dormancy (Kitchen and Meyer, unpublished data on file at the Shrub Sciences Laboratory, Provo, Utah). Rapid drying of the soil surface would make the germination of surface seeds following summer or autumn rains less likely. Buried seeds with a light requirement are functionally dormant and would contribute to the seed bank. Apparently, chilling does not reduce the light requirement in *P. palmeri* seeds, while warm incubation eliminates it in a significant fraction of the seeds (Table 3). This suggests that buried seeds may be more likely to germinate in the fall after experiencing sufficient warm incubation to eliminate their light requirement.

Whether current-year *P. palmeri* seeds germinate in the fall or spring may depend as much on time of seed dispersal as temperature and moisture conditions that follow. The collection dates for each population (Table 1) and field observations regarding the timing of fruit dehiscence suggest that populations from areas with milder winters (lower elevations) tend to ripen and disperse seed during late summer. At higher elevations where cold weather would occur earlier, seed ripening and dispersal are delayed.

Habitats with mild winters and unpredictable spring moisture seem to favor early dispersal and fall germination. Such sites select for the maintenance of a seed bank because extended periods of drought are typical and conditions for successful establishment may not be met for many years. Cold-induced secondary dormancy and burial of light-requiring seeds should facilitate the buildup of this soil seed reserve. In habitats with more severe winter conditions dispersal is retarded and spring germination of a portion of the seeds is both probable and less risky. The preservation of a seed reserve through cold-induced dormancy may also be important in these more mesic habitats.

Penstemon palmeri appears to be adapted for establishment in a variety of habitats. Two phenomena are important in this success. First, individual seeds seem to be capable of responding appropriately to different environmental stimuli. Second, variability in germination response among seeds within a population is indicative of a bet-hedging strategy increasing the chances for successful establishment across a range of variabe and unpredictable environments. Habitat-related between-population variation in germination timing mechanisms appears to be relatively unimportant.

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